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Effects of concentration and treatment duration upon dwarf pea response to gibberellic acid root treatments in solution culture

S. J. ANDERSON, W. M. JARRELL and E. FRANCO-VIZCAINO[1]
Department of Soil and Environmental Sciences, University of California, Riverside, CA 92521, USA, and [1]Centro de Investigación Científica y Educación Superior de Ensenada, Baja California, Mexico

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Abstract

Gibberellic acid (GA_3) root treatments stimulated internode elongation of hydroponically grown dwarf pea seedlings (*Pisum sativum* L., cv. Little Marvel) when the GA_3 concentration in the solution was at least 2.9 μM.

Both GA_3 concentration and the duration of the root-treatment period significantly affected internode elongation. This is attributed to a limited availability or saturation of active sites for gibberellin-induced cell elongation. The amount of GA_3 taken up through the roots in 1 day from a 29 μM GA_3 solution apparently equaled or exceeded the amount which could be metabolized during the first four days after treatment, although higher concenrations and longer treatment periods produced a more prolonged response, conceivably due to 1) initial saturation of gibberellin active sites, 2) storage of surplus gibberellin in the plant, and 3) subsequent utilization of the stored gibberellin. GA_3-induced stem elongation in hydroponically grown Little Marvel peas seemed to be limited initially by apparent saturation of active sites when the GA_3 concentration exceeded 29 μM.

Introduction

Hydroponic solutions provide the ideal growth medium for studying the effects of gibberellic acid (GA_3) root treatments upon plant growth, particularly the influence of treatment duration on the magnitude and longevity of the response to the exogenous hormone. Short (< 12 h) pulses of GA_3 added to the nutrient solution have been shown to stimulate photosynthesis in tomatoes for up to eight days after treatment (Arteca and Dong, 1981), and geranium growth is enhanced by root applications of GA_3 (Arteca *et al.*, 1985). Dwarf peas grown for at least two weeks in nutrient solutions containing 14.5 μM GA_3 were nearly 4 times taller and had greater shoot weights than control plants, though gibberellin treatment decreased root weight (Brian *et al.*, 1954). Because they lack the full complement of enzymes required for gibberellin biosynthesis, untreated dwarf pea plants are only one-half as tall as phenotypically normal plants (Allison-Creese *et al.*, 1985; Phinney, 1984; Phinney and West, 1961; Reid *et al.*, 1983). Stimulation by GA_3 of internode elongation in peas results from enhancemnet of both endomitotic and mitotic events (Callebaut *et al.*, 1980; Mohammed and Capesius, 1980). Thus, internode elongation is a morphological manifestation of the biochemical response to GA_3, including that taken up through the roots.

This paper focuses upon the threshold GA_3 concentration and treatment duration required for prolonged stimulation of internode elongation in dwarf peas. The objectives of this experiment were 1) to determine the minimum GA_3 concentration to which dwarf pea plants will respond in hydroponic solution; 2) to determine the period of time for which the roots must be exposed to this hormone in

order to produce a prolonged growth response at the whole-plant level of expression. If brief [1-, 3-, or 5-day (d)] root treatments with low solution concentrations effectively increase growth, then soil application of GA_3 might be a feasible option for some crops.

Materials and methods

Planting and transplanting

Seeds of *Pisum sativum* L., cv. Little Marvel, were obtained from Carolina Biological Supply Company (Gladstone, Oregon). The seeds were non-segregating mutants which produce phenotypically wrinkled, green, dwarf plants in the absence of exogenous GA_3. Planting and transplanting were done under a laminar-flow transfer hood using aseptic technique in order to create an initially sterile root environment and retard GA_3 biodegradation during the hormonal treatment period.

Seeds were surface-sterilized with 3% NaOCl for ten minutes and rinsed four times with sterile deionized water, ten minutes per rinse. After the fourth rinse the seeds were soaked 24 h in sterile tap water. Prior to planting the seeds, masonry sand was moistened with quarter-strength Hoagland's solution (Hoagland and Arnon, 1938), and the moist sand was put into porcelain-coated metal trays which were then covered with translucent, autoclavable polypropylene bags and autoclaved for 30 minutes at 121°C, 100 kPa. The pre-soaked seeds wre sown 2 cm deep in the sterile sand and the polypropylene covers were put back into place.

In preparation for transplanting, one-quart (0.95 l), wide-mouth mason jars were filled with 0.87 l of half-strength Hoagland's solution which had been adjusted to pH 6.2 with KOH. A 10-cm^2 piece of Teflon film (Cadillac Plastics) was placed over the mouth of each jar, and a hole 0.7 cm in diameter was cut into the center of the film. The purpose of the thin Teflon sheet was to prevent adsorption of GA_3 onto either the jar lid or the sterile cotton which was used to hold the seedlings in place. The Teflon film was covered by a jar lid into the center of which a hole 1.6 cm in diameter had been punched for a pea plant (Fig. 1). The central holes in the Teflon film and lid were concentric, and the hole in the Teflon was just large enough to permit transfer of the roots into the nutrient solution but was not large enough to allow the hypocotyl to enter the nutrient solution, while the larger hole in the jar lid allowed free passage of both the root and the hypocotyl. Each lid also contained a 1.0-cm diameter hole for the aeration system. The jar lids, held in place by screw-cap

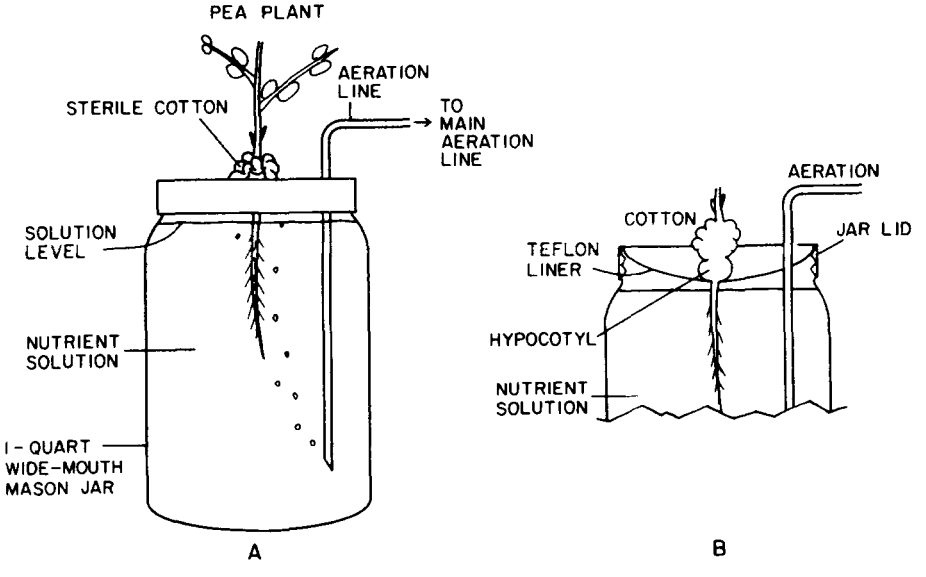
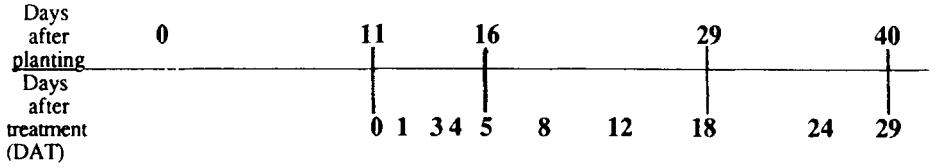


Fig. 1. **A** Mason jar apparatus used for growing Little Marvel dwarf peas. Jars were covered with aluminium foil (not shown) to keep root in dark. **B** Cross-sectional view showing position of teflon lid-liner and hypocotyl.



6 d after planting: Transplant seedlings into 0.95-L nutrient solution in mason jars.

0 DAT: Add gibberellic acid to nutrient soulutions. Measure internodes of all plants.
1 DAT: Change solutions of 1-d-treatment plants.
3 DAT: Change solutions of 3-d-treatment plants.
4 DAT: Measure internodes of all plants.
5 DAT: Change solutions of 5-d-treatment plants.
8 DAT: Measure internodes of all plants.
12 DAT: Measure internodes of all plants.
18 DAT: Measure internodes of all plants.
24 DAT: Measure internodes of all plants.
29 DAT: Measure internodes of all plants.

Fig. 2. Timing of planting, treatment, and measurement of Little Marvel peas during hydroponic experiment.

bands, were covered with aluminium foil to prevent surface contamination after autoclaving, and the jars were autoclaved for 30 minutes at 100 kPa and 115°C. No solids precipitated during or after autoclaving when the solution pH was 6.2.

Seedlings were selected for uniform shoot height and transplanted when the first true leaf began to unfold, six days after planting. The pea plants were transplanted under a laminar flow transfer hood into the mason jars. Immediately after the seedlings were transplanted, the jars were removed from the sterile transfer hood and brought into the glasshouse. Sterile aeration lines (0.6-cm i.d. neoprene tubing fitted with glass capillary tubing as flow restrictors) were inserted into the jars through the small hole in the lid, thus puncturing a tight-fitting hole in the teflon sheet. The incoming air was filtered through sterile cotton and glass wool in an effort to reduce microbial contamination. The mason jars were then wrapped with aluminium foil in order to provide a dark environment for the roots. The sterility of the roots and solutions was ascertained three days after transplanting by plating the roots and nutrient solutions of randomly selected plants onto nutrient agar; no colonies appeared on the plates after a two-week incubation.

Gibberellic acid treatments

Pea seedlings were treated with gibberellic acid (Sigma Chemical) by adding 10 ml of GA_3 stock solution (buffered at pH 6.5 with 0.005 *M* KH_2PO_4) to the nutrient solution when the third internode was just beginning to elongate, 11 days after planting. The GA_3 stock solutions were 0.246, 2.46, and 24.6 m*M* to give final nutrient-solution hormone concentrations of 2.9, 29, and 290 μM (1.0, 10, and 100 ppm) GA_3. Preliminary experiments showed no significant response to 1-, 2.5-, or 4-d treatments with lower GA_3 concentrations (unpublished data).

Plants were grown for 1, 3, or 5 days in the GA-containing nutrient solutions and then were transferred to GA-free, pH 6.2 nutrient solution (Fig. 2). The nine treatments plus a control were assigned in a random-block experimental design with six replicates per treatment. The plants were grown during May and June in a glasshouse with no supplemental lighting, and day/night temperatures were maintained at 37°C/22°C. The pH of the nutrient solution was checked every fourth day, but no adjustments were necessary because solution pH remained between 6.0 and 7.0.

Internode elongation measurements

Total internode length above the first true leaf was determined when the plants were treated, as well as 4, 8, 12, 18, 24, and 29 days after treatment (DAT) (Fig. 2). Previous work had shown no response until at least 3 days after treatment (unpublished data). The quantity "elongation response" was defined as

$$\text{Elongation response index} = \frac{\text{(Total internode elongation of treated plants)}}{\text{(Mean total internode elongation of control plants)}} \times 100.$$

Earlier experiments had shown that GA_3 root treatments did not affect root, shoot and total dry weights, C assimilation, or leaf area (non-significant differences at $p \leqslant 0.2$; unpublished data).

A 3 × 3 (concentration × time) factorial decomposition of the treatments was used for analysis of variance and interaction analysis. Standard error of the difference between means was calculated using the formula $SE_{\Delta\bar{x}} = [2(MSE)/n]^{1/2}$. Response data for 12, 18, 24, and 29 DAT were analyzed using multiple regression (Steel and Torrie, 1980). Comparisons among treatment means were made using the least significant differences test (LSD) (Snedecor and Cochran, 1980).

Results

Effect of gibberellic acid concentration

All plants treated with GA_3 for 1, 3, or 5 d showed a significant response relative to the control 4 DAT and at all subsequent measurement dates ($p \leqslant 0.05$; Table 1). The elongation response of plants treated 1, 3, or 5 d with 2.9 μM GA_3 began to decline shortly after termination of the treatment, while higher concentrations produced a more prolonged response. The magnitude of the stimulation was larger for higher concentrations for any given treatment duration, and the stimulatory effect persisted longer for higher GA_3 concentrations (Table 1).

Higher GA_3 concentrations also resulted in higher maximum elongation rates (Figs. 3a–3c). The maximum elongation rate for 1-d treatment with 2.9 μM GA_3 (8 DAT) was greater than the control, but at later dates the elongation rate for this treatment was not statistically different than the control ($p > 0.05$). The internode elongation rate of plants treated with 290 μM GA_3 for 1 d was greater than the control at all times ($p \leqslant 0.05$; Fig. 3a).

For 3-d exposure to GA_3, the principal effect of increasing the concentration beyond 29 μM was to maintain high internode elongation rates for a longer time. The elongation rate of plants treated with 290 μM GA_3 decreased only slightly between 8 and 18 DAT, whereas the rate for plants in the 29-μM treatment group decreased to approximately one-half of its maximum value during that same period (Fig. 3b). This suggests that although active sites for gibberellin-induced cell elongation initially were saturated by the 29-μM treatment, the surplus hormone taken up from the 290 μM GA_3 solution during a 3-d treatment period was either stored for later use, or its growth-promoting effects were extended over a considerable time period.

Elongation rate data for plants treated for 5 d also indicate that gibberellin active sites initially were saturated by concentrations exceeding 29 μM (Fig. 3c). As with the 3-d treatments there was no statistical difference between the elongation rates produced by the two highest concentrations 8 or 12 DAT, but 18 DAT there was a significant difference between the two highest treatments ($p \leqslant 0.01$). Because there were no differences in either plant height or rate of elongation for the 29 and 290 μM, 5-d treatments, it is suggested that the significant difference in elongation rates found 18 DAT re-

Table 1. Elongation response (percentage of mean control elongation) of dwarf pea seedlings following GA_3 treatment

GA_3 concentration μM	Treatment duration days	Days after treatment					
		4	8	12	18	24	29
2.9	1	225.2	190.7	141.6	122.2	123.2	123.2
2.9	3	271.4	260.9	196.5	147.5	141.2	141.2
2.9	5	260.4	280.3	216.2	158.3	151.0	151.0
29	1	284.9	294.5	242.1	178.4	165.6	166.2
29	3	262.0	329.0	286.5	209.5	198.8	204.2
29	5	310.7	367.8	343.9	252.8	232.0	234.7
289	1	280.6	330.7	315.3	247.0	235.9	248.8
289	3	294.6	350.2	317.9	267.3	259.2	277.2
289	5	285.8	335.8	322.1	275.0	280.0	301.7
$LSD_{0.05}$		44.7	44.3	36.7	24.2	20.4	21.8

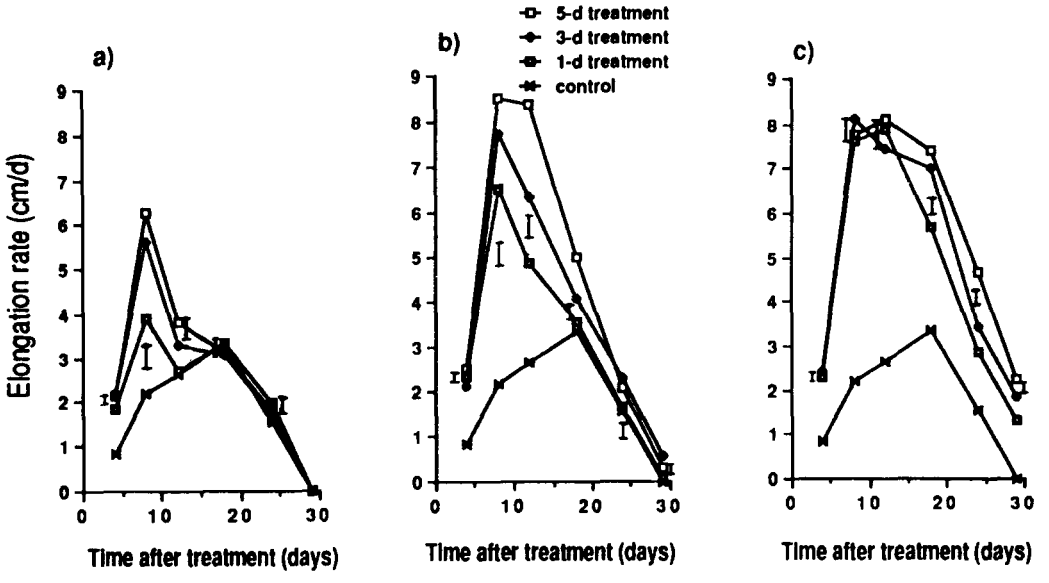


Fig. 3. Effect of GA_3 concentration upon time course of elongation rates for Little Marvel peas. Each point represents the mean of six replicates. *Error bars* denote the standard error of the difference of means. **a)** 1-d treatment; **b)** 3-d treatment; **c)** 5-d treatment.

flects different amounts of GA_3 taken up through the roots and stored by plants treated 5 d with these two gibberellin concentrations.

Because plants treated with 290 μM GA_3 for 3 or 5 days did not have higher stem elongation rates 8 and 12 DAT than plants treated for the same length of time with 29 μM GA_3, there is no simple relationship between concentration and the maximum elongation rate.

Effect of treatment duration

Total internode growth of plants treated with 2.9, 29, and 290 μM GA_3 depended upon the root-treatment duration. For the 2.9-μM treatments the time effect was most pronounced 8, 12, and 18 DAT, although there was never a statistical difference between the 3- and 5-d treatments (Table 1). With the intermediate concentration (29 μM),

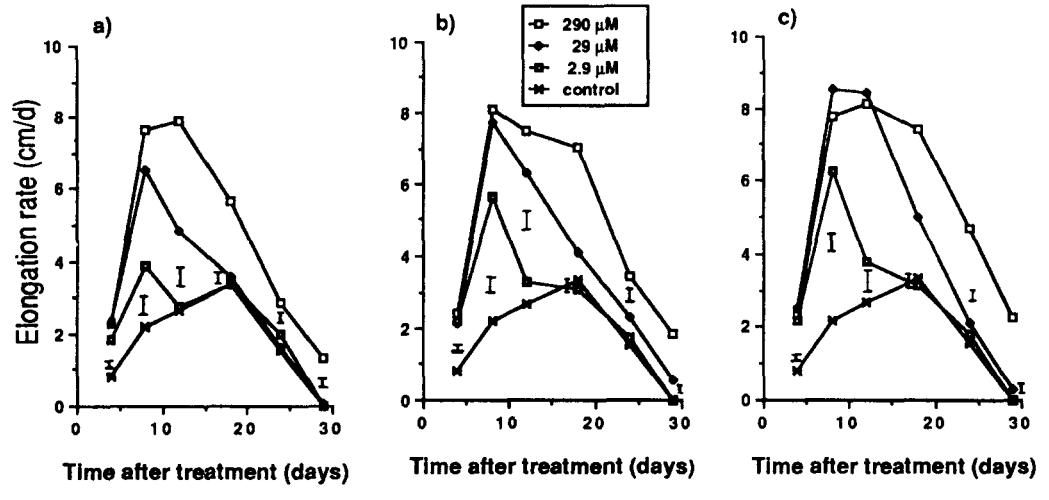


Fig. 4. Effect of GA_3 treatment duration upon time course of elongation rates for Little Marvel peas. Each point represents the mean of six replicates. *Error bars* denote the standard error of the difference of means. **a)** 2.9 μM GA_3; **b)** 29 μM GA_3; **c)** 290 μM GA_3.

treatment duration significantly affected height 12 DAT and thereafter; the height of plants treated 3 d was significantly greater than that of plants treated only 1 d, and significantly less than the height of plants treated with GA_3 for 5 d. In contrast, treatment duration did not have a statistically significant effect upon height of plants treated with 290 μM GA_3 until 24 DAT.

For low concentrations the effect of treatment duration was greatest 8 DAT, while for higher concentrations the effect was significant only at the end of the experiment. Treatment duration had the most pronounced effect upon the total internode elongation of those plants treated with 29 μM GA_3 (Table 1).

Elongation rates also were affected by treatment duration (Figs. 4a–4c). Maximum elongation rates for plants treated 3 or 5 d with 2.9 μM GA_3 were greater than for the 1 d treatment, although there was no difference ($p > 0.05$) between the 3 and 5 d treatments (Fig. 4a). Plants treated with 29 μM GA_3 for 3 and 5 d had higher maximum elongation rates than plants treated for 1 d (Fig. 4b). The internode elongation rate of plants treated 1 d with 29 μM GA_3 decreased to the level of the control 18 DAT, while the rates for longer treatment periods remained greater than the control longer into the experiment ($p \leqslant 0.05$; Fig. 4b).

In contrast, exposure period did not significantly affect maximum elongation rates of plants treated with 290 μM GA_3 ($p > 0.05$; Fig. 4c). However, beginning 18 DAT the rate for the 5-d, 190 μM treatment was nominally higher than for the 3-d treatment, which in turn gave greater elongation rates than the 1-d treatment, although those differences were not always statistically significant at $p \leqslant 0.05$.

These observations support the hypothesis that the highest GA_3 concentration may have kept all available active sites saturated until many days after the roots had been placed in a GA-free solution. One can infer from these data that when pea seedlings are grown in a nutrient solution containing 29 or 290 μM GA_3, the amount of hormone absorbed through the roots during a 3- or 5-d treatment period exceeds the quantity which can be metabolized immediately, although at least some of the GA_3 which is not immediately utilized in growth-promoting reactions appears to be stored for later use rather than being consumed in catabolic reactions. The GA_3 might be stored as a free, biologically active gibberellin, or as a conjugated gibberellin derivative. Many plants store GAs as conjugates, and enzymatic or chemical hydrolysis of these conjugates releases biologically active GAs (Schneider, 1983). Reversible conjugation, particularly of exogenous GAs, is one mechanism by which plants may control the tissue concentration of biologically active GAs (Barendse *et al.*, 1968; Schneider, 1983).

Combined effects of gibberellin concentration and treatment duration

Simple linear regression analysis. Root-treatment duration and GA_3 concentration both had highly significant ($p \leqslant 0.0001$) effects upon plant height when internodes were measured 8, 12, 18, 24, and 29 DAT. Elongation response data (Table 1) were analyzed using both simple-linear and multiple-linear regression analyses in order to ascertain the relationship between log (response) and the two independent variables gibberellic acid concentration (X_1, μM) and treatment duration (X_2, days). The regression analyses were performed using data from individual plants rather than treatment means. Simple-linear regression analysis revealed that at each measurement date the partial correlation coefficient for the relationship between response and GA_3 concentration was greater than the partial coefficient for the correlation between response and treatment duration, demonstrating that concentration was always a better single predictor of elongation response than was treatment duration (Table 2).

Multiple regression analysis. The regression coefficients of the multiple-linear regression equations (Table 2) allow comparisons of the relative importance of concentration and treatment period at different measurement dates. Although the partial correlation coefficients in the linear regressions showed that GA_3 concentration had a greater influence upon elongation response than did treatment duration, it was believed that the *relative* importance of these two variables might change with time. Such a change would manifest itself through variations in the ratio of the full-model regression coefficients (b_1/b_2) of concentration and treatment duration.

Table 2. Partial correlation coefficients and multiple regression equations for elongation response (percentage of control elongation) at different time intervals following treatment

Time after treatment (days)	Partial regression coefficients			Ratio of coefficients	
	log μM	treatment duration	Two-variable regression equation[a]	b_1/b_2	R^2
12	0.762	0.368	(1) $\log Y = 2.138 + 0.122 \log X_1 + 0.029X_2$	4.14	0.716
18	0.856	0.339	(2) $\log Y = 2.022 + 0.139 \log X_1 + 0.026X_2$	5.07	0.848
24	0.875	0.34	(3) $\log Y = 2.003 + 0.136 \log X_1 + 0.026X_2$	5.14	0.882
29	0.887	0.300	(4) $\log Y = 1.991 + 0.149 \log X_1 + 0.027X_2$	5.50	0.893

[a] Y denotes elongation response as percentage of control, X_1 represents GA_3 concentration (μM) and X_2 represents treatment duration (days).

The ratio increased from 4.1 to 5.5 between 12 and 29 DAT (Table 2), indicating that during this period elongation response was determined increasingly by GA_3 concentration and less by treatment duration. In general, the increase in the ratio b_1/b_2 appears to have risen because during the initial post-treatment period the amount of GA_3 taken up from a solution containing 290 μM GA_3 saturated available active sites and did not produce taller plants than did treatment with 29 μM GA_3. Later in the experiment (18, 24, and 29 DAT), it appeared that surplus GA_3 which had been taken up from the 290 μM solution during the treatment period was available for use in growth-promoting reactions, although it is not clear whether the GA_3 thus utilized had been stored as free GA or as a GA-conjugate.

Statistical interaction. The presence of a statistically significant interaction between gibberellin concentration and treatment duration, investigated using a 3 × 3 factorial decomposition of the nine

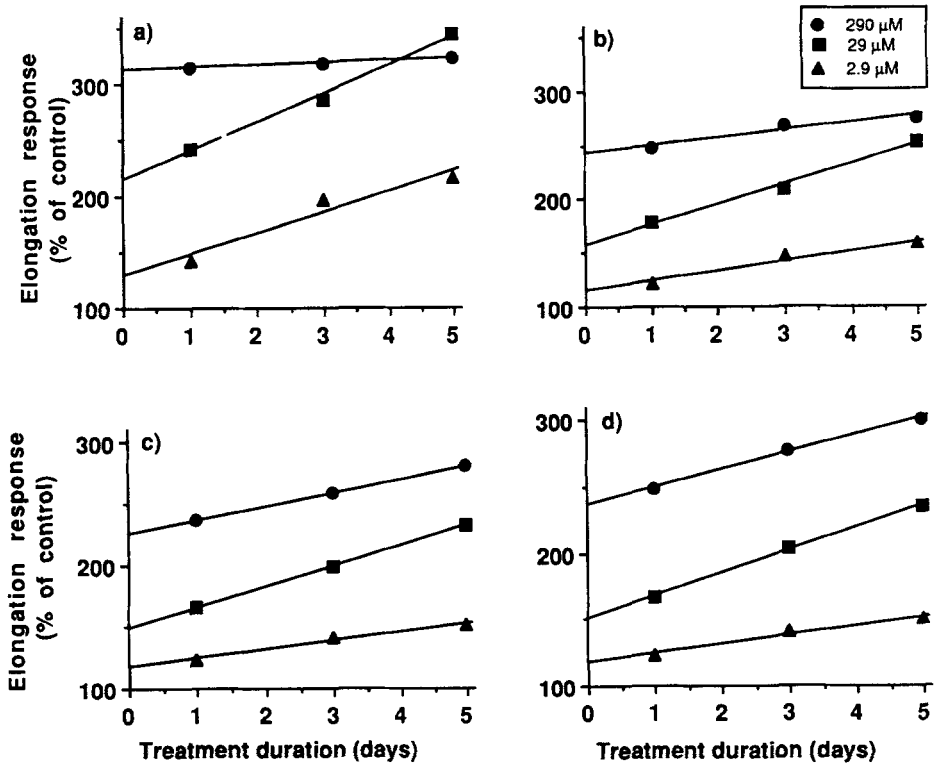


Fig. 5. Interaction between GA_3 concentration and treatment duration at various times after treatment. **a)** 12 DAT; **b)** 18 DAT; **c)** 24 DAT; **d)** 29 DAT.

treatments, indicates that plants treated with at least one of the three GA_3 concentrations responded differently to the three treatment durations than did plants treated with either of the other two concentrations. A significant interaction between dependent variables is indicated in the interaction plots (Figs. 5a–5d) if the slope of at least one of the lines in each figure is significantly different from the other two.

The interaction was most significant ($p \leqslant 0.01$) 12 DAT because elongation response for the 29-μM treatments depended significantly upon treatment duration, while root-treatment duration had no influence upon total internode elongation of plants treated with 290 μM GA_3 (Fig. 5a). The concentration × duration interaction was less significant 18 DAT ($p \leqslant 0.07$) and 24 DAT ($p \leqslant 0.10$), and was not significant ($p > 0.15$) 29 DAT.

Thus, the statistical significance of the concentration × treatment duration interaction declined monotonically at later dates. Conversely, the ratio b_1/b_2 increased with increasing time after treatment. Both of these phenomena could indicate that more GA_3 than could be utilized immediately was taken up from the 290 μM solutions, and as sites were made available to this "surplus" GA_3 many days after treatment, the regression coefficient of concentration (b_1) became greater relative to b_2, the coefficient of treatment duration. Concomitantly, the interaction between concentration and treatment duration became less significant.

Discussion

Saturation of GA_3 active sites manifests itself as a statistically significant interaction between concentration and treatment duration, and precludes the possibility that there might be a linear relationship between maximum elongation rates and GA_3 concentration. Gibberellin uptake is the rate-limiting process only during the first hours after treatment (O'Neill *et al.*, 1986), but after this initial period the amount of hormone absorbed through the roots exceeds the availability of active sites. The research reported in this paper indicates that moderately high GA concentrations saturate active sites, but the "extra" gibberellin can be stored, possibly as GA conjugates, for later use by the plant. Reversible conjugation (formation of glucosyl esters or glucosides followed by release of free GA) is believed to be a means by which plants regulate tissue concentrations of biologically active GA, although much of the evidence for this is indirect (Schneider, 1983). However, when a foreign GA is applied to peas, studies have indicated that some of the exogenous GA is stored as a polar conjugate and later released as free GA (Barendse *et al.*, 1968). In addition, recent research with high-specific-activity GA_4 and GA_{20} has shown that significant storage (reversible conjugation) of these GAs takes place during seed maturation and germination in maize (Rood *et al.*, 1983).

Garcia-Martinez *et al.* (1981) reported that the major forms of gibberellin in leaf vacuoles of cowpea and barley are GA_8 and its polar conjugate GA_8-glucoside. Other studies have shown that GAs stored as glucosides and glucosyl esters, which are readily translocated within plants, can be released by enzymic or chemical hydrolysis. Research suggests, though not unequivocally, that both endogenous and exogenous GA pools may be regulated, at least partially, by the reversible conjugation of free GAs (Schneider, 1983).

The macroscopic evidence for reversible conjugation of excess GA_3, presented in this paper, suggests that if GA_3 were applied to soils, it should be possible to elicit a desired growth response even if the GA_3 remaining in the soil were degraded by microorganisms within a few days of the hormone application.

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